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Stars in the Silurian sky: Echinoderm holdfasts from the Carnic Alps, Austria

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ABSTRACT

A small collection of echinoderm holdfasts from the Ludlow Cardiola Formation of the Carnic Alps (Austria) contains a wide range of morphologies as a response of environmental adaptation. In general, the holdfasts have a globous and massive dome-like profile with several processes arranged in a sub-radial disposition, so to create a sort of 'star-like' outline. A small central depression is common but not present on all specimens. The distinctive holdfasts are preserved in an iron-rich phase, documenting a substitution that has also affected other non-echinoderm calcareous material.

KEYWORDS | **Pelmatozoans. Holdfast. Functional morphology. Palaeoecology. Iron. Silurian. Cardiola Formation.**

INTRODUCTION

The Silurian deposits of the peri-Gondwana area are famous for their well-preserved fossils and the peculiar associations of black bituminous limestones, rich in cephalopod shells and black graptolitic shales. The presence of suitable conditions for the co-occurrence of graptolites and conodonts, primary biostratigraphical markers for the period, has enabled a precise age assignment of most of the exposed sections. Unluckily, owing to the complex sedimentological and tectonic evolution of the area, many successions are incomplete and significant parts of the Silurian may be missing.

Cephalopods are the most abundant elements in the fauna with conchs commonly oriented parallel to bedding surfaces. Bivalves, associated with brachiopods, corals, gastropods, trilobites, acritarchs and chitinozoans are present as well. Echinoderm remains are abundant, but complete specimens are extremely rare and poorly documented. Their skeletal remains may more commonly occur in such masses as to be rock-forming, like in the Late Ordovician, middle Silurian and at the Silurian/Devonian boundary.

In an attempt to document and correlate time-specific facies (sensu Brett *et al*., 2012; Ferretti *et al*., 2012a) across the Iapetus Ocean during the Silurian, our attention has focused on Silurian calcareous occurrences in the Carnic Alps, exposed south of the Mount Rauchkofel in Austria. The locality is already known in the literature for its rich palaeontological content, including recently documented laminated structures

such as the ferruginous coatings around skeletal fragments (mostly trilobites and some cephalopods and echinoderms) and stromatolitic features along discontinuity surfaces that are interpreted as evidences of Silurian microbial activity (Ferretti, 2005; Ferretti *et al.*, 2012b). In order to improve the biostratigraphical resolution based on conodonts (Schönlaub, 1980), samples of limestone were collected and etched in dilute formic acid. A small association of echinoderm holdfasts was recovered in the acid residue. Pelmatozoan holdfasts have relatively rarely been studied on their own (see among others Franzén, 1977; Brett, 1981; Donovan *et al.*, 2007; Plotnick *et al.*, 2016). Despite the fact that holdfasts are commonly preserved dissociated from their column and calyx, holdfast morphology provides important information on the palaeoecology of pelmatozoan echinoderms and on conditions at the sediment-water interface (*e.g.*, Seilacher and MacClintock, 2005; Zamora *et al.*, 2010; Thomka and Brett, 2015). The purpose of the present paper is to describe, illustrate and assess the significance of this fauna.

GEOLOGICAL SETTING

The Carnic Alps, located across the Italian-Austrian border (Fig. 1), expose one of the most complete Palaeozoic successions in the world, ranging in age from the Middle Ordovician to the Late Permian. During the early Palaeozoic, the Carnic Alps were part of the group of terrains (Galatian terranes; von Raumer and Stampfli, 2008) that detached from the northern Gondwana margin in the Ordovician and moved northward faster than the main continent, from about 50ºS in the Late Ordovician to 35ºS in the Silurian and to the tropical belt in the Devonian (Schönlaub, 1992). This is reflected in clear differences in litho- and biofacies along the Carnic Alps.

Rocks from the Middle Ordovician to the lower Pennsylvanian that were affected by the Variscan orogeny during the late Bashkirian and Moscovian (Venturini, 1990; Schönlaub and Forke, 2007) constitute the so-called Pre-Variscan sequence. The lithostratigraphy of this sequence was significantly revised recently, and 36 formations are now formally discriminated in the Pre-Variscan sequence of the Carnic Alps (Corradini and Suttner, 2015). For a recent description of the geology of the Carnic Alps, refer to Corradini *et al.* (2015c, 2016).

Silurian deposits are irregularly distributed within the Carnic Chain and range from shallow water bioclastic limestones to nautiloid-bearing limestones, interbedded shales and limestones, to deep-shelf or basinal black graptolitic shales and cherts ('lydites'). The overall thickness does not exceed 60m. The Silurian transgression started at the base of the Llandovery, and, due to the disconformity separating Ordovician and Silurian strata, an unknown thickness of sedimentary rocks is locally

FIGURE 1. Location map of the Rauchkofel Boden Section.

missing, which corresponds to several conodont zones of Llandovery to Ludlow age (Schönlaub and Histon, 1999; Brett *et al.*, 2009; Corradini *et al.*, 2015a).

Three calcareous units are present in the proximal parts of the basin: the Kok Formation (Telychian-lower Ludfordian), the Cardiola Formation (Ludfordian), and the Alticola Formation (upper Ludfordian-basal Lochkovian). These units correspond mostly to the '*Orthoceras* limestones' of earlier authors and are represented by bioclastic wackestones-packstones. Nautiloid cephalopods are abundant. Trilobites, bivalves and conodonts are common; crinoids, gastropods and, more rarely, ostracods, brachiopods and chitinozoans are present as well (Corradini *et al.*, 2003, 2010, 2015a; Ferretti, 2005; Brett *et al.*, 2009; Histon, 2012a, b). The black graptolitic shales with interbedded cherts and clay-rich alum shales of the Bischofalm Formation were deposited in the deeper part of the basin. Intermediate sedimentary conditions between calcareous and shaley facies are represented by the Nölbling Formation, comprised of alternating black graptolitic shales, marlstones and limestone beds.

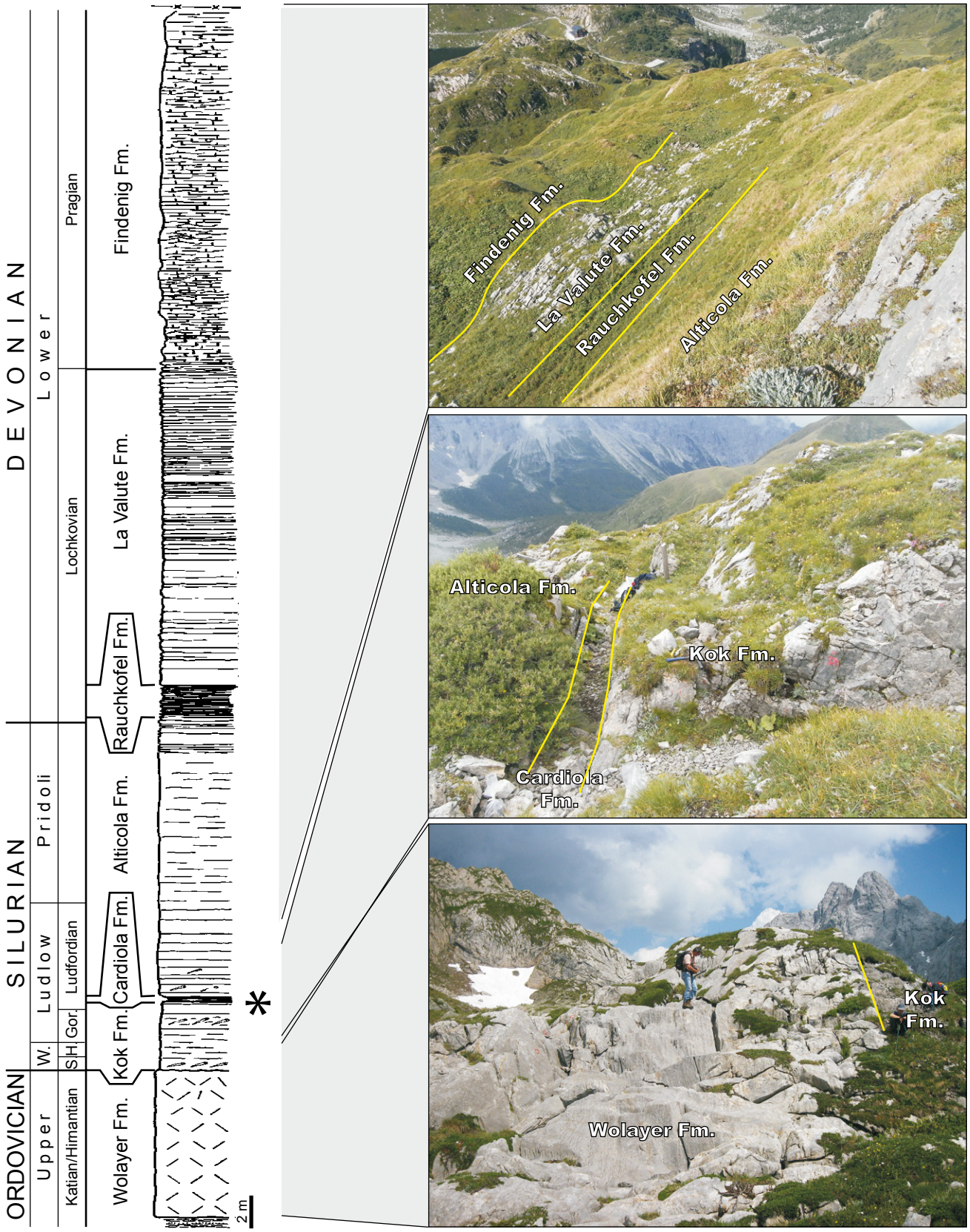

FIGURE 2. Chronostratigraphy, lithostratigraphy, stratigraphical log (modified after Schönlaub, 1980) and selected views of the Rauchkofel Boden Section. The asterisk indicates the level from which the studied material was collected. Gor.: Gorstian; H.: Homerian; S.: Sheinwoodian; W.: Wenlock.

The Rauchkofel Boden Section

The Rauchkofel Boden Section (Fig. 2) is located on the southwestern slope of Mt. Rauchkofel, at coordinates N 46º36'54", E 12º52'30" and an altitude of 2175m. Approximately 65m of rocks from Upper Ordovician to Lower Devonian in Wolayer facies are exposed here, but a significant gap is present in the lower Silurian, embracing almost the whole Llandovery. The Rauchkofel Boden Section is one of the best known sections of the whole Carnic Alps, and numerous studies and monographic works have been carried out. In addition to a detailed descriptions of the section, sedimentology, sequence stratigraphy and geochemistry, papers concentrate on nautiloid cephalopods, trilobites, bivalves, conodonts, corals, dacryoconarids and Problematica. For a summary see Ferretti *et al.* (1999), and for an up-to-date litho- and chronostratigraphical description refer to Corradini *et al.* (2015b). The conodont biostratigraphical frame was provided by Schönlaub (1980) and Ferretti and Schönlaub (2001) and is currently under revision by some of the authors of this paper.

Seven formations, formally introduced recently, are exposed in the Rauchkofel Boden Section: the Wolayer Formation (Late Katian to ?basal Hirnantian), the Kok Formation (Telychian-lower Ludfordian), the Cardiola Formation (Ludfordian), the Alticola Formation (upper Ludfordian-basal Lochkovian), the Rauchkofel Formation (Lochkovian), the La Valute Formation (Lochkovian) and the Findenig Formation (uppermost Lochkovian-Eifelian). The Rauchkofel Boden Section represents the stratotype of both the Wolayer and the La Valute formations.

FIGURE 3. Slab of Cardiola Fm. showing the peculiar cardiolid bivalve-cephalopod association. Scale bar corresponds to 5cm.

The Cardiola Formation

The studied material was collected from the Cardiola Formation (Fm.) (Fig. 3), constituted by dark gray to black shales with limestone intercalations as thin planar to hummocky-laminated, fine-grained calcareous beds and calcisiltites. In the Rauchkofel Boden section the Cardiola Fm. is poorly exposed in the World War I trench, and its thickness is limited to 30-40cm. In other parts of the Carnic Alps, the unit may reach up to 4m.

The depositional environment in which the Cardiola Fm. and, in general, the black cephalopod limestone occurrences were deposited along the peri-Gondwana area has been a matter of strong debate. The absence of a real benthic shelly fauna coupled with the presence of bivalve-dominated communities of the *Cardiola*-Community Group, comprised mostly of epibyssate forms, and the abundant organic matter and the peculiar bituminous smell have attracted different speculations. According to Ferretti and Kříž (1995), a surface current present below normal wave base was temporarily ventilating the sea-bottom and distributing bivalve, gastropods and other fauna larvae along with empty cephalopod shells over the region. Cardiolid bivalves had adapted their morphology and feeding strategy, developing three prominent points distributed at the vertix of a triangle in order to attach to cephalopod conic conchs deposited on the bottom and representing a firm substrate (Kříž, 1979, 1998, 1999). Oxygen concentration was, however, apparently limited as no true brachiopod and trilobite dominated communities are present.

STARS IN THE SILURIAN SKY

Material and methods

We have obtained a small fauna of echinoderm holdfasts from a conodont residue from the Silurian (early Ludlow) Cardiola Fm. of the Rauchkofel Boden Section in the Austrian Carnic Alps. The specimens were hand picked under a Zeiss Stemi SV 11 binocular microscope from a limestone which had been processed with diluted formic acid, sieved with a 100µm net and dried. No further concentration methods were applied. The echinoderm holdfasts were common in the residue, generally well preserved, and complete. Microfracturing and cleavage of the specimens were rarely observed. A peculiar reddish colour was revealed in optical microscopy (Fig. 4). Optical microscope photographs were taken under a Wild Heerbrugg M8 stereomicroscope using a Nikon Coolpix 990. A few specimens were coated with gold and were observed

with an Environmental Scanning Electron Microscope FEI ESEM-Quanta 200, equipped with an Oxford EDX INCA 300 X-ray energy dispersive spectrometer system. X-ray powder diffraction (XRPD) was collected on selected samples at room conditions on randomly oriented powdered samples using a Philips X'Pert PRO diffractometer equipped with an X'Celerator detector.

Optical microscopy, XRPD, and ESEM-EDX analyses were performed at the 'Centro Interdipartimentale Grandi Strumenti' (CIGS) of the University of Modena and Reggio Emilia (Modena, Italy). The material on which this paper is based is reposited in the Palaeontological Collections of the Dipartimento di Scienze Chimiche e Geologiche, Università degli Studi di Modena e Reggio Emilia, under repository numbers IPUM 28992-29022.

Other faunal elements

The echinoderm holdfasts have been recovered from a conodont residue that also included other faunal elements. Abundant trilobites, cardiolid bivalves, brachiopods, sponge spiculae, ostracodes, gastropods, echinoderm ossicles and nautiloid embryonic chambers were recovered as well (Fig. 5). Surprisingly, all the faunal elements have been preserved in the same iron-rich phase detected for the echinoderm holdfasts. Trilobites are rarely complete, and in general the all material appears well sorted and equidimensional. Muellerisphaerida or the enigmatic *Eurytholia* plates (Ferretti *et al.*, 2006; Ferretti and Serpagli, 2008) and unassigned phosphatic rings (Ferretti *et al.*, 2013) documented in the level immediately above the top of the Cardiola Fm., have not been found.

Biostratigraphical assignment

The conodont fauna includes *Polygnathoides siluricus* Branson and Mehl, 1933 (Fig. 5A), *Kockelella variabilis variabilis* Walliser, 1957 (Fig. 5B), *Kockelella variabilis ichnusae* Serpagli and Corradini, 1998, *Wurmiella excavata* (Branson and Mehl, 1933), *Panderodus unicostatus* (Branson and Mehl, 1933) and anomalous elements with branched processes (Corradini *et al.*, 1996; Corradini and Corriga, 2010; Slavik, *et al.*, 2010; Corriga *et al.*, 2014). This association allows a precise assignment of the level to the lower part of the *P. siluricus* Zone, before the LADs of *K. v. variabilis* and *K. v. ichnusae* that became extinct in the lower part of the Zone (Ludfordian, Ludlow) (Serpagli and Corradini, 1999; Corriga *et al.*, 2009, 2014; Slavík *et al.*, 2010; Corradini *et al.*, 2015a).

Mineralogical composition

As previously remarked, the faunal association picked in the residue has a peculiar rusty appearance,

FIGURE 4. Optical stereomicroscope images of echinodermal holdfasts IPUM 28992a-i from the Cardiola Fm., Rauchkofel Boden Section, Austria. Note the reddish colour of the material. Scale bar corresponds to 1mm.

with colour ranging from a dark red to a deep brown (Fig. 4). Furthermore, the elements have magnetic properties and can be easily picked from the residue by the use of a magnet. Apparently, only the originally calcareous organisms have this 'iron- rich' preservation. Phosphatic elements such as conodonts keep their usual aspect and mineralogical composition. Analyses by XRPD revealed that the red material consists of the iron oxyhydr-/oxides goethite (α-$Fe^{3+}O(OH)$) and magnetite ($Fe^{3+}{}_2Fe^{2+}O_4$).

The pelmatozoan holdfasts are preserved as a thin layer of ferruginous material. Because the stereomic microstructure (Figs. 6D; 7C) and some of the details of the column facet (Fig. 7H) are preserved, it appears that the outler layer of the original specimen was replaced by the iron-rich phases. The centre of the specimens is not preserved (Fig. 7C-D, J-K) and it was dissolved away either during later diagenesis or during the formic acid sample processing.

Description

The presence of stereomic microstructure (Figs. 6D, 7C) demonstrates that these holdfasts are from an echinoderm, as do the pentameral symmetry aspects preserved in a few specimens. These include a coarse subpentagonal outline of the column facet opening on Figure 6B, the pentalobate column facet opening in Figure 7F and the pentagonal opening on Figure 7H. The presence of these holdfasts and isolated columnals indicates that these holfasts are from some pelmatozoan echinoderm. The absence in our material of pelmatozoan remains other than holdfasts and columnals makes any taxonomic identification beyond pelmatozoan echinoderm speculative.

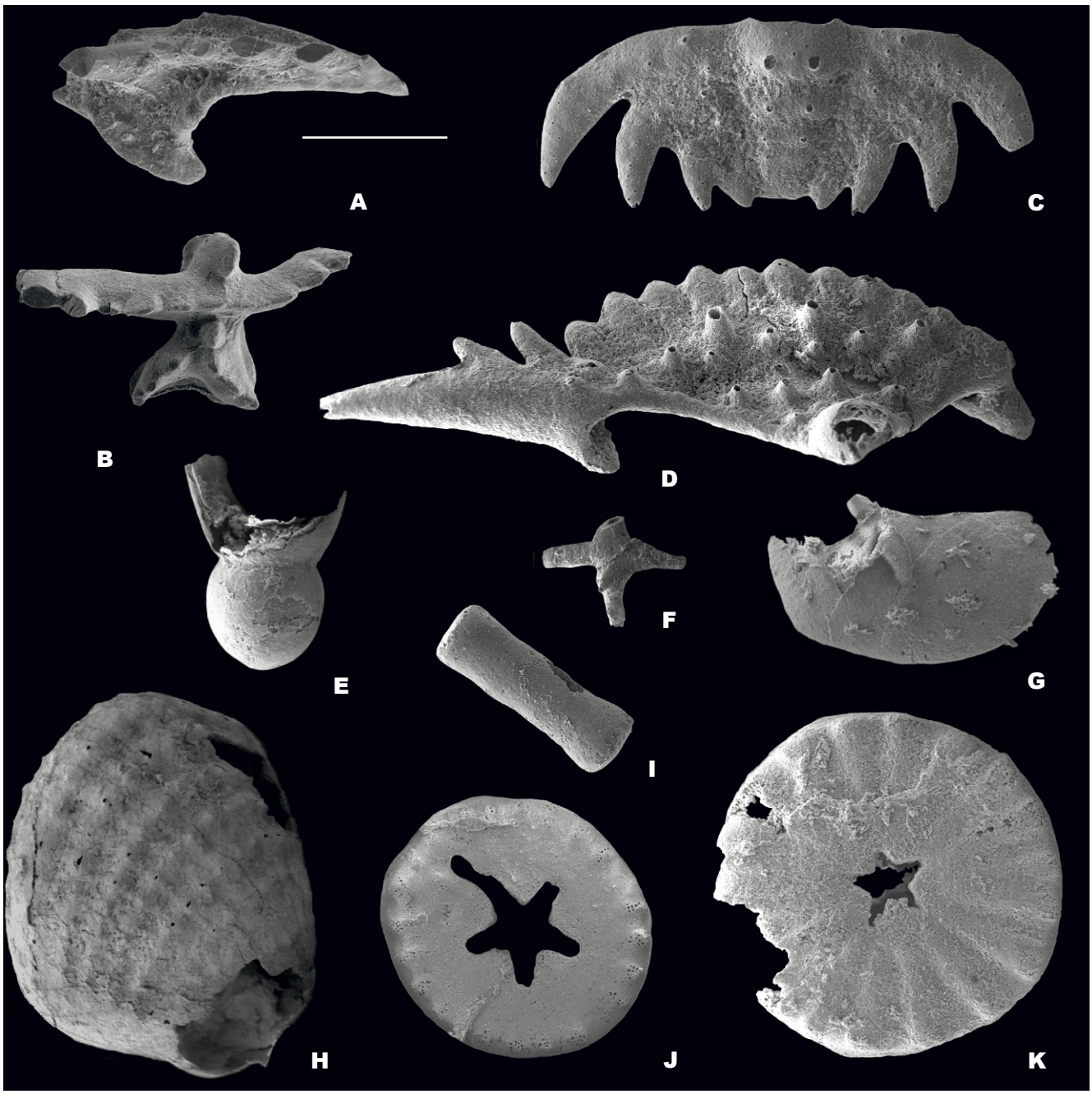

FIGURE 5. Scanning electron micrographs of main faunal elements from the Cardiola Fm. of Austria. A) *Polygnathoides siluricus* Branson and Mehl, 1933, upper view of P2 element IPUM 28993. B) *Kockelella variabilis variabilis* Walliser, 1957, upper view of P1 element IPUM 28994. C-D) oral views of trilobite fragments, specimen IPUM 28995 and IPUM 28996. E) nautiloid embryonic chamber, specimen IPUM 28997. F) Sponge spicula, specimen IPUM 28998. G) Ostracode with overgrowth of pyrite crystals, specimen IPUM 28999. H) Articulated cardiolidid bivalve, specimen IPUM 29000. I-K) Echinoderm ossicles, specimens IPUM 29001-29003. Scale bar corresponds to 500μm.

Echinoderm holdfasts of our material range in dimension from 1 to 4mm, with a mean value of 2mm, and the column facet diameter on the holdfasts ranges in size from 290 to 425μm. As a general feature, the specimens apparently have a globous body with a flat surface (here regarded as the lower one) and a bulbous opposite dome (here regarded as the upper part). Therefore, in lateral view, specimens are nearly truncate conical shapes (Fig. 6J). Some holdfast systems have a more curved basal surface and a thinner lateral curved profile, with branches departing and growing in opposite directions (Fig. 8B, F). Some others have a distinctive flat discoidal profile (Fig. 6H). No vertically oriented branches possibly indicating penetration into a soft sediment were recognized.

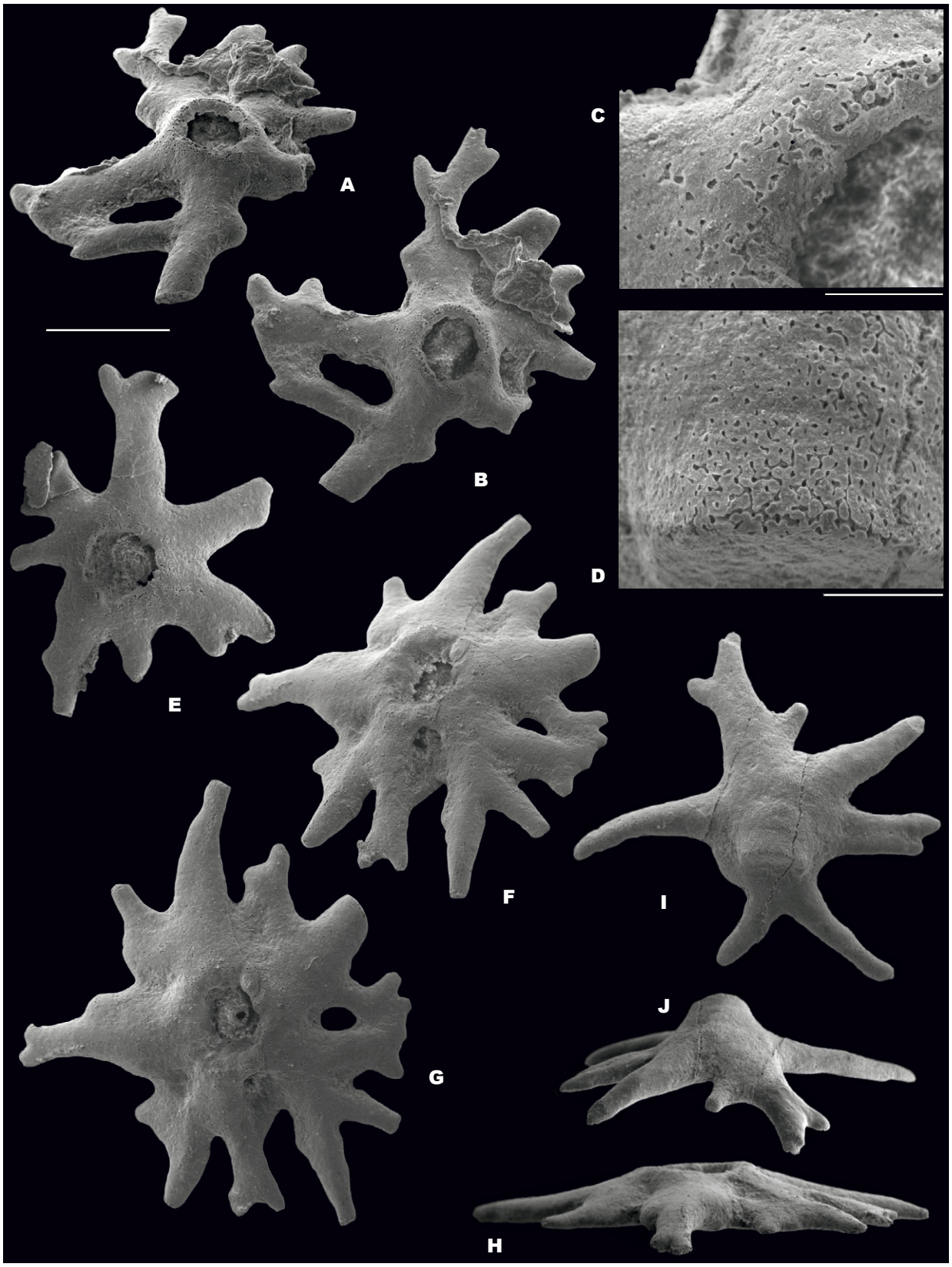

FIGURE 6. Scanning electron micrographs of Silurian pelmatozoan holdfasts. All specimens are from the Cardiola Fm. of Austria. A-B) Sub-lateral and oral views of specimen IPUM 29004. C-D) Details of specimen IPUM 29004 and specimen IPUM 29005 showing the typical stereom pattern of echinoderms. E) Oral view of specimen IPUM 29006. F-H) Sub-lateral, oral and lateral views of specimen IPUM 29007. I-J) Oral and lateral views of specimen IPUM 29005. Scale bars correspond to 500μm in all frames except C-D where bars represent 100μm.

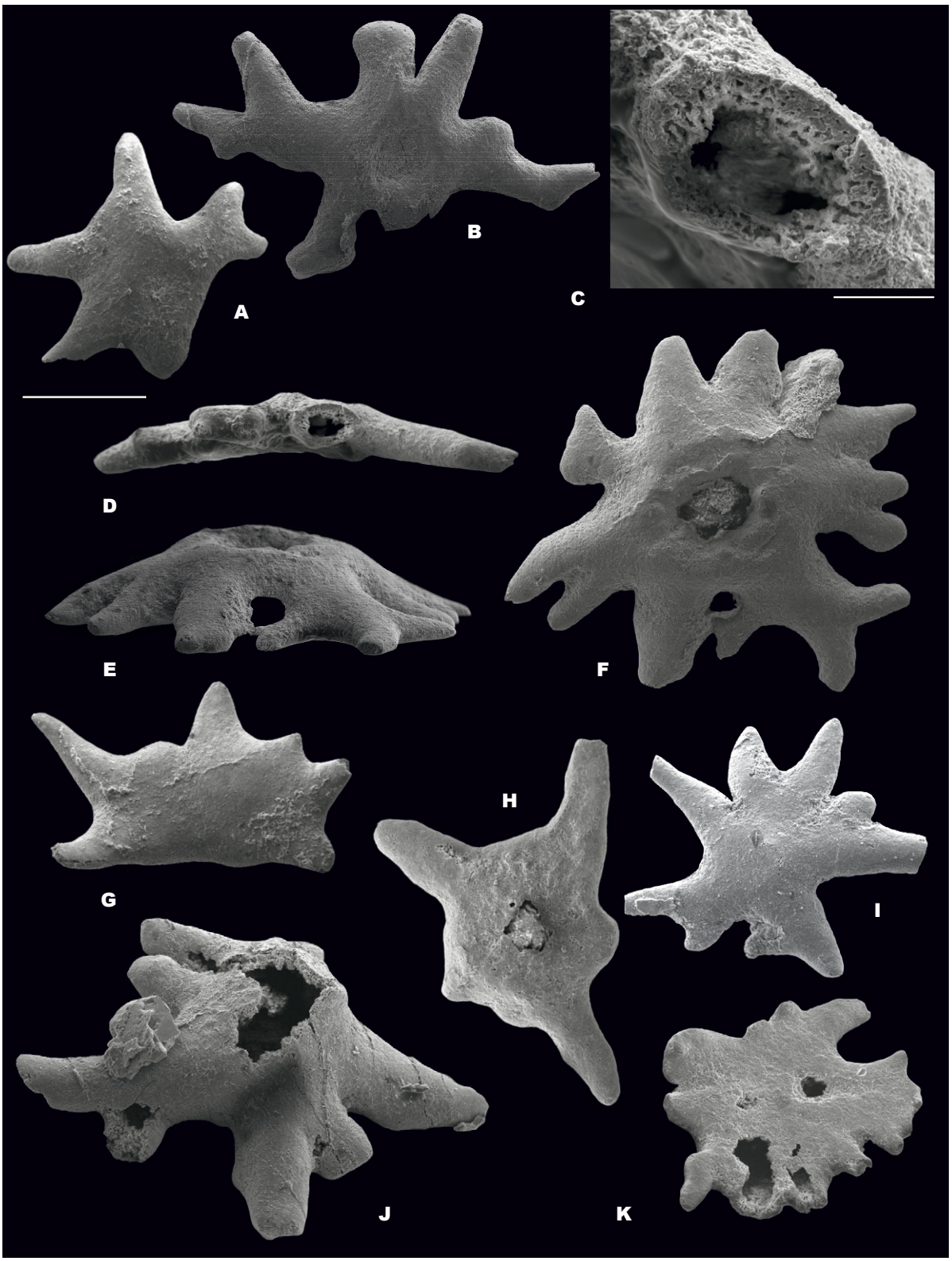

FIGURE 7. Scanning electron micrographs of Silurian pelmatozoan holdfasts. All specimens are from the Cardiola Fm. of Austria. A) Oral view of specimen IPUM 29008. B, D) Oral and lateral views of specimen IPUM 29009. C) Detail of D showing a hollow process in specimen IPUM 29009. E-F) Lateral and oral views of IPUM 29010. G) ?Oral view of specimen IPUM 29011. H) Oral view of specimen IPUM 29012. I) Oral view of specimen IPUM 29013. J) Sub-lateral view of specimen IPUM 29014. The breakage of the holdfast in the apical part reveals that the main body is empty. K) Aboral view of specimen IPUM 29015, showing again the hollow central part. Scale bars correspond to 500μm in all frames except C where bar represents 100μm.

From above, the holdfast has a subcircular outline with several branches irregularly departing from the centre and delineating a sort of star. Branches may be up to 12 in number. A recent paper (Plotnick *et al.*, 2016) has described a distinctive preferred geometric pattern in branch distribution in holdfast of the mid-Palaeozoic *Eucalyptocrinites*. However, no precise symmetric patterns may be detected in our material, with processes that appear to be arrayed in all directions, but keeping a subordinate radial signal. Just a few specimens have a straight unbranched side, possibly as a response of the presence of a nearby holdfast that has prevented growth in that direction (Fig. 8I-J). A couple of specimens have four processes and developed a quadrilobate symmetry (Fig. 8C), which may be secondarily infilled as growth processes (Fig. 6F-G). Processes are commonly short and massive, more rarely slender and elongate or creating a dendritic net-like arrangement (Fig. 6B). Each branch is separate from the other and sometimes is partly overlapping the following one (Fig. 8E) or merging at mid length, delineating circular holes between processes (Figs. 6G, 7F, 8K). Processes are circular in section and bifurcated at its proximal end (Fig. 7F) or expanding in a bulbous terminal enlargement (Fig. 7B) to possibly increase adhesion to the substrate. Holdfasts are internally hollow both in the basal body (Fig. 7J-K) and inside the processes (Fig. 7C).

Most of the echinoderm holdfasts have a central depression, not reaching the basal part. The central lumen has a general circular outline with conical borders (Fig. 6A). On a few specimens, a geometric design may be detected (pentalobate in Fig. 7F and pentagonal in Fig. 7H). Some other elements lack the median depression (*e.g.*, Fig. 7G). On a number of specimens, there is clear evidence of a median raised area (Figs. 6D, I-J, 8C-D) instead of the central lumen. Finally, in spite of the mineral substitution that has occurred and possibly obliterated primary structure, no evidence of segmentation and/or articulation of different ossicles was detected in any specimen, suggesting a massive original architecture of the holdfast.

DISCUSSION

Attachment structures in pelmatozoan echinoderms may be very helpful for understanding the paleoecological setting. Brett (1981, 1984) identified three major modes of fixation to the substrate as a response to specific environmental conditions. In his terminology (1981, tab. 1, p. 348), the holdfasts under investigation would be included in terminal stem holdfasts.

Pelmatozoan holdfasts are known from settings including hardgrounds (Brett *et al.*, 1983), skeletal substrata (Ausich and Wilson, 2016), firmgrounds (Zamora *et al.*, 2010), and soft substrata (Seilacher and MacClintock, 2005) (among many references). The affinities of most isolated holdfasts are not known; however, in relatively rare cases complete specimens are preserved. Three examples are eocrinoids from the Cambrian of northern Spain (Zamora *et al.*, 2010), Ordovician crinoids from North America (*e.g.*, Brower, 2005), and *Caryocrinites* from the Silurian of North America (Brett, 1978). Dendritic, encrusting holdfasts with a similar morphology to the specimens from the Cardiola Fm. have been reported from many localities and have been attributed to many groups (*e.g.*, Brett, 1978; Hollis and Ausich, 2009; Sumrall *et al.*, 2015; Thompka and Brett, 2015; Ausich and Wilson, 2016). However, holdfasts in the studies mentioned above are mostly from adult pelmatozoans and contrast sharply in size with the very small, undoubtedly juvenile pelmatozoans reported from the Cardiola Formation.

Recently, the complete development of a living stalked crinoid, *Metacrinus rotundus* Carpenter, 1885, has been documented (Amemiya *et al.*, 2014), so comparisons between living and fossil juveniles can now be made. The earliest developmental phase of a crinoid is a free-living larva, which eventually settles to the substratum and attaches to a hard surface where it begins a benthic existence as a small, attached, stemmed echinoderm. The earliest post-larval phase lacks arms and is referred to as the cystidean stage. When the initial arms begin to grow, the post-larval crinoid is considered to be part of the pentacrinoid stage. In living comatulid crinoids, the crown autotomizes to yield a free-living animal. Adult stalked crinoids that had a holdfast other than a cemented holdfast autotomized at least the juvenile, attached holdfast. This is true among living isocrinoids and for many fossil crinoids (*e.g.*, Hollis and Ausich, 2009).

In the living crinoid *Metacrinus rotundus*, the middle to late cystidean stage had column diameter immediately above the holdfast of approximately 130µm, whereas this column diameter was approximately 215µm by the early pentacrinoid stage (Amemiya *et al.*, 2014). The Cardiola Fm. holdfasts have a facet for the distal-most columnal that ranges from 290 to 425µm. Thus, assuming that parallels can be drawn between *Metacrinus rotundus* and Palaeozoic pelmatozoans, the Cardiola holdfasts are interpreted to be from the middle to late pentacrinoid stage or somewhat older juvenile forms. These pelmatozoans were probably from individuals between the smallest and larger juvenile crinoids reported from the Devonian Hunsrück Slate (see Kammer *et al.*, 2015, fig. 2 versus fig. 1B).

All of the holdfast specimens are preserved isolated from the surface to which they were attached during life. Because organisms in this fauna with original

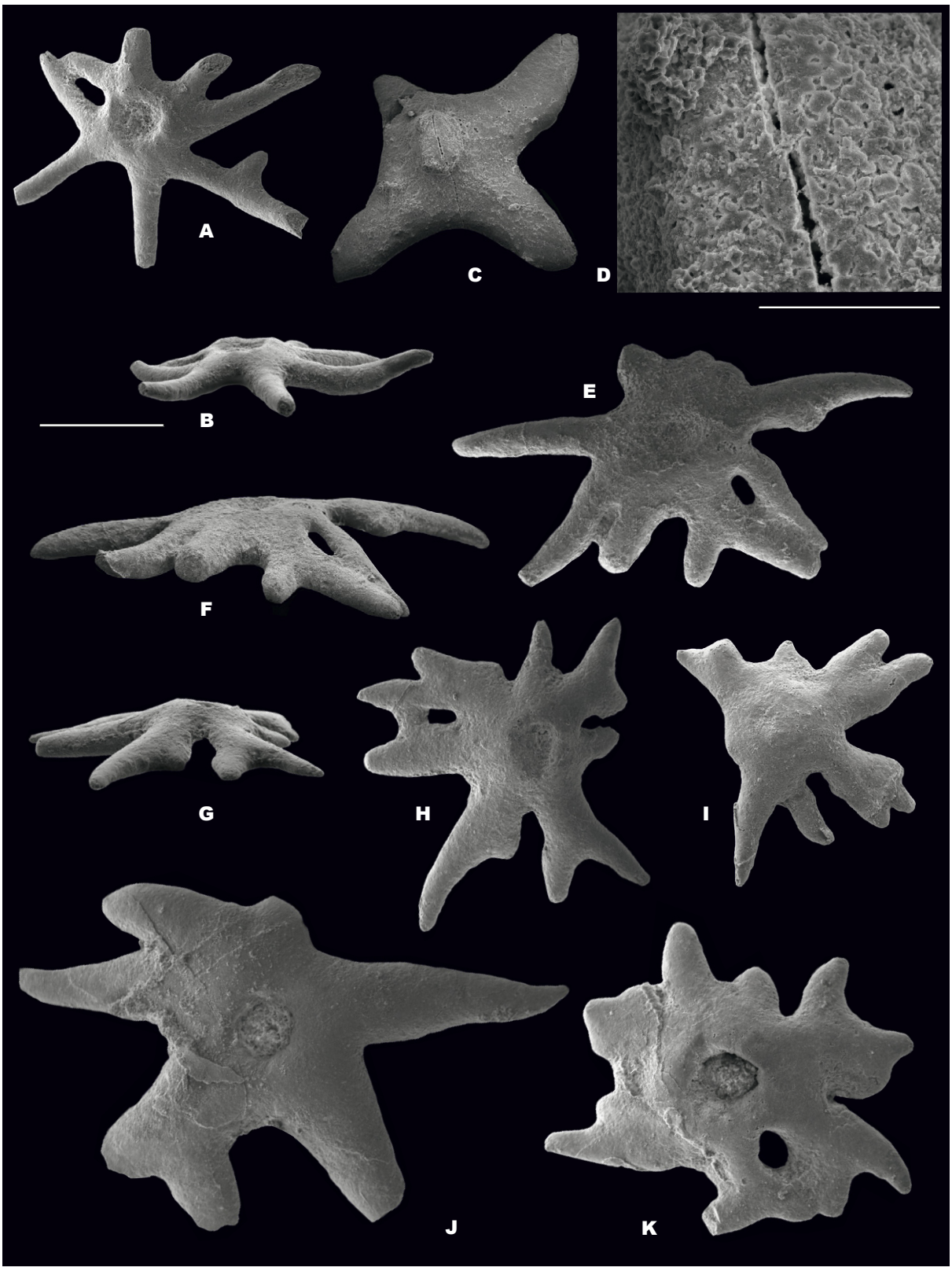

FIGURE 8. Scanning electron micrographs of Silurian pelmatozoan holdfasts. All specimens are from the Cardiola Fm. of Austria. A-B) Oral and lateral views of specimen IPUM 29016. C) Oral view of specimen IPUM 29017. D) detail of C illustrating the stereom pattern in the central apical ridge. E-F) Oral and lateral views of specimen IPUM 29018. G-H) Lateral and oral views of specimen IPUM 29019. I) Oral view of specimen IPUM 29020. J) Oral view of specimen IPUM 29021. Note the pyrite crystal overgrowth on the left. K) Oral view of specimen IPUM 29022. Scale bars correspond to 500μm in all frames except D where bar represents 100μm.

calcite skeletal material are preserved in iron oxyhydr-/oxides, it is probable that when alive, these holdfasts were attached to either an aragonitic shell or to a soft-bodied organism, such as algae. It is likely that these pelmatozoans lived in the Cardiola Fm. setting because these holdfasts are absent in adjacent facies. However, it is also possible that they were introduced into the Cardiola assemblages as pseudoplanktonic organisms attached to a swimming cephalopod shell or to floating algae.

The base of the stem was moderately elevated above the substrate. In most examples, the posture of the column (based on the orientation of the holdfast lower surface) was vertical or near vertical to the substratum when the column was attached. However, the column of the holdfast illustrated in Figure 6I was at a high angle to the substratum, suggesting that this holdfast was attached to the side of an object with relief.

The Cardiola Fm. holdfasts are interpreted to be from a juvenile pelmatozoan. Because the morphology of these juveniles overlaps with morphologies in adults of more than one clade of pelmatozoan echinoderm, a more specific identification is not possible.

CONCLUSIONS

A large number of ferruginous pelmatozoan echinoderm attachment structures has been recovered in the Silurian Cardiola Fm. in the Austrian Carnic Alps. Documented holdfasts design a massive discoidal appearance with a general simple pattern of branching. Processes on our material are shorter and relatively thicker if compared to other Silurian occurrences, which may be expected for juvenile holdfasts (*e.g.*, Plotnick *et al.*, 2016). Their dominant flat lower surface would suggest adhesion to a planar firm bottom substrate.

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